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THE LIFE HISTORY OF THE CARPENTER ANT.

JOHN LOSSEN PRICER.

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INTRODUCTION.

The studies reported in this paper were undertaken originally with the purpose of applying to another species of ants some of the tests and experiments which have yielded interesting results to other investigators, and incidentally I have been led to endeavor to work out the life history of a colony. In respect to the ecology of my species I have not aimed at completeness in any division, but have taken up whatever was at once most available under my conditions and most promising of results within the time at my disposal.

The work was done in the graduate school of the University of Illinois, as a part of the requirement for the degree of Master of Arts, and under the immediate supervision of Dr. S. A. Forbes, to whom I am deeply indebted for his many kindly and helpful suggestions and criticisms.

MATERIAL AND METHODS.

Two varieties of *Camponotus herculeaneus* — *C. pennsylvanicus*, and *C. ferrugineus* — were made the basis of this work. So far as I have been able to learn, these varieties have exactly the same habits, the only difference noted being that *C. pennsylvanicus* is slightly more abundant in this region than the other variety.

The colonies used in my experiments were, for the most part,

collected from various small tracts of woodland within three or four miles of Urbana. These colonies were placed, after collection, in artificial nests of the Fielde type (BIOLOGICAL BULLETIN, Vol. II., No. 2), and were kept throughout the winter in a room of the insectory of the state entomologist, which is on the university campus. This room is heated by steam and was kept during the winter at a fairly constant temperature, ranging from 70° to 90° F. The ants were fed on sweetened water, pieces of insects, cooked lean meat, boiled eggs, etc., and all seemed to thrive perfectly on this fare.

My experiments were modeled after those of Fielde, Lubbock and others, but were usually modified in some details, in order to adapt them better to the species used; and a few experiments were specially devised to follow up and verify the conclusions arrived at. One outdoor colony was studied rather closely from about July 1, 1906, until their activities ceased with the approach of cold weather. All the work was done during the academic year of 1906-07, and all dates given in this paper are of this year.

LIFE HISTORY OF A COLONY.

Believing that a knowledge of the complete life history of such perennial colonies as are formed by the ants under consideration might throw considerable light on other important topics, I have undertaken to do what I could to work it out. The problem is a difficult one to handle in the short time of one collegiate year, and my results are necessarily incomplete.

My methods have been as follows :

1. I captured queens which had not settled in permanent quarters after their marriage flight, and placed them in artificial nests to rear their first season's brood of callows. I compared these small colonies as to number, size and general character of the individuals with many other similar colonies found in natural outdoor nests.

2. Throughout the winter I collected as many larger colonies as possible and carefully counted both the adult ants of all forms, and the larvæ. These colonies were collected when the temperature was low enough to make them inactive, so that by care-

fully chopping to pieces the logs, stumps and trees in which they were found, I was able to obtain the colonies almost entire. Some colonies were counted as they were first picked up, and others were killed in cyanide bottles and counted later.

As a result of the first method I have the following data :

On July 10, 1906, I found a dealated queen of *C. pennsylvanicus* crawling on the sidewalk in the university campus. I placed her in a Fiedle nest in a basement room of the insectory and observed her daily throughout the summer and autumn. For the first three days she remained in the light room as if not content with her lot, but she then went to the dark room and on July 18, I saw the first eggs. Eggs were laid, in all, as follows :

| | |
|---------------|----------------|
| July 18.....2 | July 24.....2 |
| " 19.....3 | " 25.....1 |
| " 20.....2 | " 26.....2 |
| " 21.....2 | " 27.....1 |
| " 22.....2 | " 28.....2 |
| " 23.....2 | August 1.....1 |

These eggs hatched as follows :

| | |
|-----------------|-----------------|
| August 11.....2 | August 16.....2 |
| " 12.....3 | " 17.....1 |
| " 13.....2 | " 18.....2 |
| " 14.....2 | " 20.....1 |
| " 15.....3 | " 22.....2 |

Two eggs did not hatch, but either dried up or were eaten. The first larvæ to appear grew very rapidly, almost doubling in size in a single day, and the rate of growth decreased gradually as other larvæ appeared to demand food and care. By September 1, the change in size was scarcely perceptible in a week's time.

These larvæ pupated as follows :

| | |
|-------------------|--------------------|
| September 1.....2 | September 10.....1 |
| " 3.....1 | " 12.....1 |
| " 4.....1 | " 16.....1 |
| " 5.....1 | " 25.....1 |

As twelve callows appeared, three more larvæ must have pupated, but the dates of their pupation are not known. The twelve pupæ gave the imago as follows :

| | | |
|--------------------|-----------------|------------------|
| September 22.....2 | October 2.....1 | October 15.....1 |
| “ 25.....1 | “ 5... ..2 | “ 19..... 1 |
| “ 27.....1 | “ 8.....2 | “ 20.....1 |

A few more eggs were laid during September, so that there were 14 small larvæ in the nest on October 15. These did not grow perceptibly until January, and then only slightly. During that month and at intervals afterwards, the queen laid a few eggs, and by May 1, the colony consisted of 15 callows, 21 larvæ and 8 eggs.

Taking the time required for the development of the first two callows as an approximate average, we have the following periods for the different stages: egg 24 days, larva 21 days, and pupa 21 days, making a total of 66 days from egg to adult. These periods are doubtless all liable to be affected by temperature and other varying conditions, for in outdoor nests some larvæ spend the winter in a state of arrested development, and I have kept one colony — No. 2, Table I. — in an artificial nest all winter in the insectory and no growth could be noticed in the larvæ until about March 1, when they suddenly began to grow at about the usual summer rate. On February 20 I gave five freshly laid eggs to a small colony with neither queen nor larvæ. Three of these hatched March 24, 28 and 30, respectively. The other two failed to hatch. These results show considerable variation in the length of the pupal period.

Another dealated queen of *C. pennsylvanicus* found on the sidewalk July 15 and placed in a nest, began laying eggs five days later, and continued at about the same rate as the one above mentioned, until twelve in all were laid. The first two of these eggs hatched August 13, an incubation period exactly the same as that of the first two eggs of the other queen. At this time the nest was allowed to become too dry and these two larvæ died and four of the eggs were destroyed. Four callows finally reached maturity, however, and the queen laid eggs at intervals throughout the winter, but was not very successful in bringing them to the adult form.

A little sweetened water was kept constantly in the nests of these two colonies and pieces of insects and some other forms of proteid food were occasionally given them, but from the time of

capture until several days after the first callows emerged I did not see either of them take food, neither was there at any time any apparent diminution of their food supply. For several days at a time I gave them only the merest drop of sweetened water, to see whether they would make a meal of it or not, but I could



FIG. 1¹. A piece of linden bark showing a cavity in which a queen of *C. pennsylvanicus* and her first season's brood of callows were found.

see no evidence that any of it was eaten. This observation, taken together with the fact that a number of outdoor colonies of sizes similar to these were found sealed up in small cavities with no communication with the outside world, as shown in Figs 1 and 2, confirms the conclusions of McCook and others that young queens take no food while rearing their first callows.

In addition to these two colonies, reared from the start in artificial nests, I have collected and counted those represented by Tables I. and II.

¹The photographs for the illustrations were taken by Dr. C. F. Hottes, Professor of botany in the University of Illinois.

It is evident from the small range in the numbers of workers and larvæ, and from the similarity of these outdoor colonies in this respect to the two described above, that all the colonies rep-

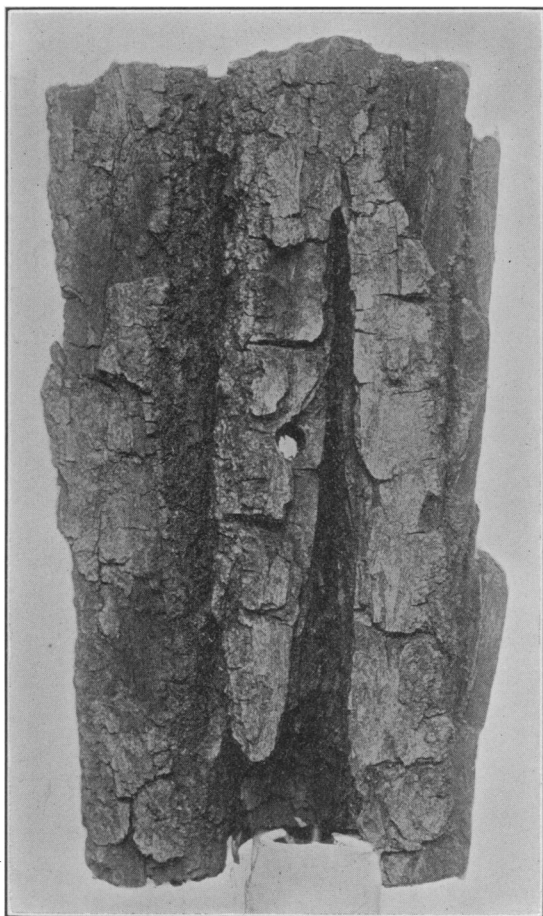


FIG. 2. Same as Fig. 1, showing hole through which the queen found entrance to the cavity.

resented in the tables below were established during the summer of 1906. The difference in the number of individuals in the different colonies is probably due to the fact that the queens left their parental nests at different times, with different amounts of reserve food, and met with various vicissitudes in their efforts to

establish new colonies. Hence we may safely regard these as colonies of one season's development, or one year old colonies.

TABLE I.

SMALL COLONIES OF *C. pennsylvanicus*.

| No. | Date. | Situation. | No. Queens. | No. Workers. | No. Larvæ. |
|-----|---------|--------------------|-------------|--------------|------------|
| 1 | Oct. 20 | Decayed oak stump. | 1 | 27 | 21 |
| 2 | Nov. 3 | Oak stump. | 2 | 23 | 32 |
| 3 | " | Cherry stump. | 1 | 13 | 18 |
| 4 | Dec. 28 | Linden log. | 1 | 3 | 12 |
| 5 | Feb. 9 | Ash stump. | 1 | 15 | 18 |
| 6 | " | Oak stump. | 1 | 7 | 10 |
| 7 | " | Cherry stump. | 1 | 3 | 12 |
| 8 | Feb. 16 | Decayed oak log. | 1 | 15 | 18 |
| 9 | " | Oak stump. | 1 | 22 | 30 |
| 10 | " | Linden log. | 1 | 8 | 18 |
| 11 | " | " " | 1 | 3 | 10 |
| 12 | " | " " | 1 | 4 | 19 |
| 13 | " | " " | 1 | 5 | 11 |
| 14 | " | Oak stump. | 1 | 11 | 20 |
| 15 | " | Ash log. | 1 | 6 | 9 |
| 16 | " | Linden log. | 1 | 2 | 15 |
| 17 | " | Hickory stump. | 1 | 4 | 18 |
| 18 | " | Linden log. | 1 | 7 | 25 |
| 19 | Mar. 9 | Hickory log. | 1 | 18 | 32 |
| 20 | " | " " | 1 | 4 | 14 |
| 21 | " | Hickory stump. | 1 | 13 | 21 |
| 22 | " | Oak stump. | 1 | 16 | 17 |
| 23 | " | Cherry stump. | 1 | 3 | 8 |
| 24 | " | Poplar log. | 1 | 4 | 18 |
| 25 | Mar. 23 | Oak stump. | 1 | 13 | 18 |
| 26 | Apr. 6 | Linden log. | 1 | 4. | 12 |
| 27 | " | " " | 1 | 7 | 13 |
| 28 | " | " " | 1 | 21 | 20 |
| 29 | " | " " | 1 | 17 | 20 |
| 30 | " | Oak stump. | 1 | 9 | 10 |
| 31 | " | Linden stump. | 1 | 5 | 11 |
| 32 | " | " " | 1 | 9 | 8 |
| 33 | Apr. 13 | Linden log. | 1 | 9 | 21 |
| 34 | " | " " | 1 | 7 | 13 |
| 35 | " | " " | 1 | 8 | 17 |
| 36 | " | " " | 1 | 3 | 14 |
| 37 | " | " " | 1 | 7 | 15 |
| 39 | " | Hickory log. | 1 | 19 | 22 |
| 40 | Apr. 20 | Linden log. | 1 | 2 | 15 |
| 41 | " | " " | 1 | 24 | 30 |

For the remaining years of the life of a colony we shall have to depend on my second method, and this will give unsatisfactory results, especially because of the limited number of data which I have been able to collect. These data are presented in Tables III. and IV.

In addition to these data I have the following miscellaneous notes :

1. May 20, 1906, I caught a winged queen of *C. pennsylvanicus*, crossing the sidewalk on the University campus.

2. June 12, 1906, I came upon a hollow tree with a small opening at the base. Around this opening were fifty or more male ants of *C. ferrugineus* in a state of great excitement, and the workers were dragging them back into the nest.

TABLE II.

SMALL COLONIES OF *C. ferrugineus*.

| No. | Date. | Situation. | No. Queens. | No. Workers. | No. Larvæ. |
|-----|---------|----------------|-------------|--------------|------------|
| 1 | Feb. 9 | Oak stump. | 1 | 15 | 25 |
| 2 | " " | " " | 1 | 7 | 19 |
| 3 | Feb. 16 | " " | 1 | 6 | 17 |
| 4 | " " | Hickory log. | 1 | 9 | 15 |
| 5 | " " | Linden log. | 1 | 10 | 21 |
| 6 | " " | " " | 1 | 3 | 14 |
| 7 | Mar. 9 | Hickory log. | 1 | 7 | 15 |
| 8 | " " | Oak stump. | 1 | 12 | 26 |
| 9 | Mar. 23 | Hickory stump. | 1 | 5 | 13 |
| 10 | Apr. 6 | Linden log. | 1 | 7 | 12 |
| 11 | " " | " " | 1 | 15 | 23 |
| 12 | " " | " " | 1 | 4 | 10 |
| 13 | " " | " " | 1 | 9 | 19 |
| 14 | " " | Linden stump. | 1 | 11 | 21 |
| 15 | Apr. 13 | Linden log. | 1 | 6 | 13 |
| 16 | " " | " " | 1 | 5 | 11 |
| 17 | Apr. 20 | Cherry log. | 1 | 13 | 26 |
| 18 | " " | Linden log. | 1 | 2 | 16 |
| 19 | " " | " " | 1 | 19 | 30 |

3. A friend told me of a colony of *C. pennsylvanicus* which inhabited a sill of his house and threw large quantities of particles of wood into his cellar. A large number of winged forms were seen about the outer opening of the nest about the first of July, and again about the middle of the same month.

4. July 6, 1906, I chopped in pieces a small decayed ash log and found a large colony of *C. pennsylvanicus* in it. Besides the workers there were probably 150 males, a large number of larvæ of all sizes, and approximately 200 pupæ, mostly of queens. About 50 workers, 30 pupæ, 20 larvæ and 15 males were taken and placed in a nest in the insectory. All the larvæ died before pupation, but seven queens and four workers emerged from the pupæ and lived through the winter in the nest. The queens emerged on the following dates :

| | | |
|---------------|----------------|----------------|
| July 25.....1 | July 281 | August 5.....1 |
| " 27.....1 | " 30.....2 | " 7.....1 |

TABLE III.

LARGE COLONIES OF *C. pennsylvanicus*.

| No. | Date. | Situation. | No. Work-ers. | No. Wingless Queens. | No. Winged Queens. | No. Males. | No. Larvæ. | No. <i>X. cava</i> . |
|-----|---------|----------------|--------------------|----------------------|--------------------|------------|------------|----------------------|
| 1 | Sep. 4 | Apple tree. | 2,500 ¹ | None seen | 200 | 150 | 300 | 0 |
| 2 | Apr. 13 | Oak log. | 3,018 | 1 | 196 | 174 | 842 | 27 |
| 3 | Mar. 9 | Oak tree. | 2,609 | 1 | 207 | 116 | 486 | 4 |
| 4 | Mar. 9 | Oak log. | 1,943 | None found | 104 | 102 | 235 | 3 |
| 5 | Apr. 20 | Linden log. | 2,291 | 1 | 0 | 0 | 123 | 2 |
| 6 | Feb. 9 | Hickory tree. | 2,139 | 1 | 0 | 0 | 867 | 0 |
| 7 | Nov. 23 | Boxelder tree. | 1,872 | 1 | 0 | 0 | 216 | 7 |
| 8 | Nov. 15 | " " | 1,246 | 1 | 0 | 0 | 196 | 2 |
| 9 | Apr. 6 | Linden log. | 1,104 | 1 | 0 | 0 | 165 | 0 |
| 10 | Apr. 20 | " " | 998 | 2 | 0 | 0 | 823 | 0 |
| 11 | Apr. 13 | " " | 886 | 1 | 0 | 0 | 171 | 0 |
| 12 | Apr. 6 | Linden stump. | 237 | 1 | 0 | 0 | 127 | 2 |
| 13 | Apr. 13 | Linden log. | 167 | 1 | 0 | 0 | 74 | 0 |
| 14 | Apr. 13 | " " | 139 | 1 | 0 | 0 | 74 | 0 |
| 15 | Apr. 6 | Linden stump. | 122 | 1 | 0 | 0 | 106 | 0 |
| 16 | Mar. 9 | Oak log. | 119 | 1 | 0 | 0 | 97 | 0 |

TABLE IV.

LARGE COLONIES OF *C. ferrugineus*.

| No. | Date. | Situation. | No. Work-ers. | No. Wingless Queens. | No. Winged Queens. | No. Males. | No. Larvæ. | No. <i>X. cava</i> . |
|-----|---------|-------------|---------------|----------------------|--------------------|------------|------------|----------------------|
| 1 | Dec. 28 | Ash tree. | 3,212 | 1 | 233 | 176 | 724 | 14 |
| 2 | Apr. 13 | Cherry log. | 2,631 | Not found | 224 | 91 | 243 | 116 |
| 3 | Apr. 20 | Linden log. | 2,214 | 1 | 131 | 97 | 322 | 51 |
| 4 | Apr. 20 | Oak log. | 2,196 | 1 | 199 | 209 | 127 | 43 |
| 5 | Mar. 23 | " " | 2,332 | 1 | 24 | 0 | 1,330 | 7 |
| 6 | Apr. 6 | Linden log. | 327 | 1 | 0 | 470 | 75 | 22 |
| 7 | Apr. 13 | " " | 143 | 1 | 0 | 0 | 87 | 7 |
| 8 | May 4 | " " | 106 | 1 | 0 | 0 | 93 | 0 |

5. In the trees of the block in which I live are eleven colonies of *C. pennsylvanicus*. These colonies were observed almost daily after the first week of July until they ceased their activities with the approach of cold weather. Between July 18 and August 12 one of them, a very large colony, was seen daily to carry empty queen pupa cases from the nest. All the other ten colonies were watched carefully during this period, but only worker pupa cases were ever seen about them. The queens which were reared in

¹ The numbers in this colony are only estimated, as the ants were too active to permit of an accurate count.

the colony remained in the nest all winter, for I never saw any evidences of swarming, and two winged queens and one male were seen crawling about the nest on the evening of October 21.

6. On November 23 a friend who lives at Delavan, Illinois, discovered a large colony of *C. pennsylvanicus* which was living in a chest of small drawers which had been left undisturbed for three years in an old unused wood shed. This colony contained both males and winged queens.

From an inspection of Tables III. and IV. it will be seen, first, that with the exceptions of colony 6, Table IV., only the larger colonies contained the winged forms during the winter, and that all the largest colonies did contain them. In addition to this some of the larvæ of two of the large colonies which did not contain winged forms, viz., colonies 6 and 7, Table III., and which were kept in nests in the insectory after capture, proved to be male larvæ, and in both these colonies, moreover, the workers laid many eggs during the winter. As the queens of both colonies died soon after capture, the eggs that appeared in the nest must have been those of workers. It has been fairly well established that the eggs of workers usually develop into males, and hence one may be certain that these two colonies would have produced males during the summer of 1907 had they been left undisturbed; and since, as the tables show, winged forms of both sexes usually occur at the same time, it is quite probable that they would have produced queens.

Putting together the foregoing observations we may draw some more or less definite conclusions.

1. In two observed instances queens appeared in the adult form during the latter part of July and the first part of August, and in one of these instances these queens emerging at this time remained in the parental outdoor nest over winter.

2. One winged queen of *C. pennsylvanicus* was observed out of the parental nest on May 20; a colony of *C. ferrugineus* was seen in the act of swarming on June 12; and a colony of *C. pennsylvanicus* was reported to have swarmed during July.

3. All of the colonies of Tables I. and II. must have been established at least as early as July.

4. Nearly all the larger colonies were found to contain winged forms of both sexes during the winter.

5. None of the ten colonies of intermediate size which were observed closely during July and August were seen to carry queen pupa cases from the nest, and only one colony of this type represented in Tables III. and IV. contained winged forms during the winter.

These facts make reasonably evident the following conclusions:

First, that a colony does not produce winged forms until it is more than two years old.

Second, that a brood of winged forms is produced during one summer, remains in the parental nest over winter, and leaves for the marriage flight during a time ranging from May to July.

In regard to the number of years required for a colony to reach sufficient maturity to produce sexually perfect individuals I have the following data:

1. The two queens which reared their first young in artificial nests laid eggs at the rate of about two a day, during the regular season, and several others taken during the winter with small colonies have laid eggs at about the same rate part of the time since being brought into the insectory.

2. In the sixty colonies of Tables I. and II. the largest number of workers in any one colony is twenty-seven, and the largest number of larvæ is thirty-two.

3. In Tables III. and IV. we have the following rather distinct groups of colonies as regard size:

(a) Eight, with the number of workers ranging from one hundred and six to two hundred and thirty-seven, and the number of larvæ from seventy-four to one hundred and twenty-seven.

(b) Four, with the number of workers ranging from eight hundred and eighty-six to twelve hundred and forty-six, and the number of larvæ from one hundred and sixty-five to eight hundred and twenty-three. The colony with the largest number of larvæ, however, possessed two queens.

(c) Three, with the number of workers ranging from eighteen hundred and seventy-two to twenty-two hundred and ninety-one, and the number of larvæ from one hundred and twenty three to eight hundred and sixty-seven.

(d) Nine, with winged forms and with the number of workers ranging from nineteen hundred and forty-three to thirty-two hundred and twelve.

4. As I shall show in more detail later under polymorphism, the workers which a queen produces the first season are all of the very smallest size and, as the colony increases in size, larger and larger workers are produced until, in colonies of the size in group (*b*) above, a few of the largest size appear.

5. As I shall show later, under division of labor, these largest sized workers seem to take no part in the work of gathering food for the colony, but remain in the nest and seem to possess largely the instincts of queens.

6. Colonies 6 and 7, Table III. and colony 1, Table IV., were kept in artificial nests in the insectory after capture, and the workers laid eggs abundantly during the winter and a large number of these eggs developed into males.

7. Two smaller ones, 8 and 16, of Table III., were also kept in the insectory after capture, without queens, and were fed just the same as those mentioned above and no eggs were seen with either of these.

These data make reasonably evident the following conclusions :

1. Sexually perfect individuals are not produced until the colony consists of approximately two thousand workers, and they are produced by nearly all colonies of this size or larger.

2. From three to six years or longer are required for a colony to reach this size.

The fact that neither eggs nor pupæ are found in the nest during the winter, and that the larvæ are all very small, must mean that the proper feeding of the young larvæ and the egg laying cease several weeks before the temperature is too low for the process of incubation. This is supported by the fact that colony 1, Table III., which was taken on September 4, contained neither eggs nor pupæ, and only very small larvæ. The cessation of these two processes is probably caused by the workers and queens storing up food in their own bodies for the processes of metabolism during hibernation. If so, egg laying and the feeding of the youngest larvæ probably cease at about the same time, and the winter larvæ are hatched from the eggs which are in the nest when the queen stops laying. Hence we have in the number of winter larvæ an indefinite clue to the rate of egg laying in colonies of different sizes. The average number of larvæ in the

colonies of Tables I. and II. is 17.5 ; in those of group (*a*) it is 94 ; for the five queens of the four colonies of group (*b*) it is 271 ; in group (*c*) it is 402 ; and in group (*d*) it is 512. Doubtless a large number of the larvæ of the last two groups and possibly of one of the colonies of group (*b*) came from eggs laid by workers. This makes it reasonably evident that eggs are laid by the queen somewhat more rapidly after the first season than during that period when, as shown above, the rate is about two eggs a day. It is also evident that while the queen alone is laying eggs and it is quite probable that the workers do not lay eggs until just previous to the time of the production of winged forms the increase in numbers is slow enough to require several years to reach the two-thousand mark. Without arguing further a point based on uncertain evidence, I feel safe in believing that the colonies of Tables I. and II. are all one year old ; those of group (*a*) are two years old ; those of group (*b*) three years old ; of group (*c*) four years old ; and of group (*d*) five or more years old. Varying conditions may make the time of development of a colony vary, and so I feel sure that the time required for a colony to reach maturity is from three to six years.

As to the life of a colony after it reaches maturity I have the following data :

1. The average number of winged forms in the colonies of Tables III. and IV. which possessed them was 292. The queen larvæ especially must require a great deal more nourishment than worker larvæ, and after reaching maturity these forms remain in the nest for three or four months of warm weather and must be fed by the workers. Thus a large portion of the energy of the colony is consumed in rearing and feeding forms which annually leave it.

2. Colony 1, Table IV., contained a large number of winged forms when collected, and after these winged forms were removed from the colony, the workers laid a large number of eggs some, at least, of which developed into males. Thus it is probable that when colonies once begin to produce winged forms they continue to do so year after year. If this is true, the constant drain thus caused on the energies of the colony might cause it to degenerate in size, if the older workers should die faster than young ones

are produced. That in this way the life of a colony may come to a natural end, is supported by the following observations :

1. On June 12, 1906, I came upon a large oak tree which was hollow at the base, and was inhabited by a colony of *C. ferrugineus*. Fifty or more males were seen about the opening of the nest in a state of great excitement and the workers were dragging them back into the nest. About a month later I revisited the tree and not a single ant was seen about the place, although I watched it for about two hours. Twice afterwards I visited the tree with the same result.

2. November 3, 1906, I tore to pieces a large oak stump which was so badly decayed that I could break it to pieces with my hands. It was thoroughly riddled by the work of insects of various kinds, and showed plainly that it had recently been inhabited by a colony of *C. pennsylvanicus*, for besides the characteristic appearance of the galleries, I found fragments of workers' bodies, a few pieces of the wings of queens, and five live males and three large workers. Plainly a colony had recently moved from the place or had there reached the natural end of its life.

3. Colony 6, Table IV., with its 327 workers and 475 males, was very likely a degenerate colony which had about reached the end of its life. This colony was found in an old linden log which was so badly decayed and riddled by galleries which had evidently at different times been occupied by the colony, that it was just about to fall in pieces, and the whole scene presented every appearance of age. As is shown in Table VI., under "polymorphism," this colony contained a comparatively very large per cent. of the largest sized workers and a very small per cent. of the smallest sized workers, and this also is an indication that the colony had existed longer than the natural life-time of the small-sized workers which are produced in such a large proportion the first two years. The large-sized workers were produced later in the life of the colony and hence we might expect to have a larger per cent. of them in a degenerate colony.

POLYMORPHISM.

The principal value of a knowledge of the complete life-history of a colony is, I believe, in the light which it will throw on the

problem of polymorphism among ants in general a problem on which much has been done and much written, but which I think, has not hitherto been examined from this standpoint.

The form of polymorphism we find here is what Eschreich in his "Die Ameise" calls incomplete polymorphism. That is, there is no distinct soldier-type, and there is a regular gradation in the size of the workers from the very largest to the smallest,

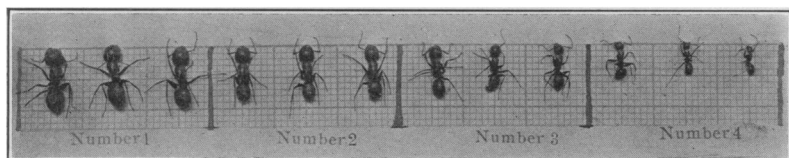


FIG. 3. Workers of *C. pennsylvanicus* arranged according to size and division of labor.

as shown in Fig. 3. I have grouped the twelve sizes shown in this figure into four subgroups to which I shall refer as Nos. 1, 2, 3 and 4, as indicated in the figure. This division into groups, I shall attempt to show later, is in harmony with an incomplete division of labor that exists among the workers.

The point revealed by a study of the life-history of a colony that I think is of importance is the fact that these different sizes of workers, and finally the winged forms, are produced at rather definite periods during the life of the colony. This is shown in Tables V. and VI.

The colonies represented in these tables were all killed in cyanide bottles and were then divided as accurately as possible into groups according to the four sizes represented in Fig. 3.

In all the colonies represented in Tables I. and II. every one of the workers was of size No. 4, and in the smaller colonies of Tables V. and VI., which, according to our previous conclusion, were two years old, this size still very largely predominated. In this latter group of colonies were found, however, a small number of size No. 3, and a still smaller number of No. 2, but not a single No. 1. From this point on, so far as the tables go, all sizes were found in all the colonies, and with the exception of colony 6, Table IV., not any perceptible increase is shown in the per cent. of the largest sized workers as the colony increased in

size, yet this per cent. varied within a narrow range for the different colonies. The fact that none of the largest size appeared in the one and two year old colonies cannot be merely accidental, for if all these colonies represented in the tables were taken together they would form a large colony, and yet not a single individual of size No. 1 would be found among them, while in the largest colony of Table V. there were 77 of this size.

TABLE V.

C. pennsylvanicus.

| No. of Colony in Table III. | Workers Size No. 1. | | Workers Size No. 2. | | Workers Size No. 3. | | Workers Size No. 4. | | Total No. of Workers. | No of Larvæ. | No. Winged Queens. | No. Males. |
|--------------------------------|---------------------------|--------------|---------------------------|--------------|---------------------------|--------------|---------------------------|--------------|--------------------------|--------------|-----------------------|------------|
| | No. | Per Cent. | No. | Per Cent. | No. | Per Cent. | No. | Per Cent. | | | | |
| 15 | 0 | 0 | 11 | 9.0 | 17 | 13.9 | 94 | 77 | 122 | 106 | 0 | 0 |
| 14 | 0 | 0 | 2 | 1.4 | 11 | 7.9 | 126 | 90.6 | 139 | 74 | 0 | 0 |
| 13 | 0 | 0 | 5 | 3.0 | 27 | 16.4 | 132 | 80.5 | 164 | 74 | 0 | 0 |
| 11 | 21 | 2.4 | 80 | 9.0 | 212 | 23.9 | 573 | 64.7 | 886 | 171 | 0 | 0 |
| 10 | 19 | 1.9 | 123 | 12.3 | 313 | 31.4 | 541 | 54.2 | 998 | 823 | 0 | 0 |
| 5 | 26 | 1.2 | 127 | 5.5 | 478 | 20.9 | 1,660 | 72.4 | 2,291 | 123 | 0 | 0 |
| 2 | 77 | 2.5 | 575 | 19.0 | 1,385 | 45.8 | 981 | 32.5 | 3,018 | 1,042 | 196 | 174 |

C. ferrugineus.

| | | | | | | | | | | | | |
|---|----|-----|-----|------|-------|------|-------|------|-------|-----|-----|-----|
| 8 | 0 | 0 | 7 | 6.7 | 28 | 26.4 | 71 | 66.9 | 106 | 93 | 0 | 0 |
| 6 | 23 | 7.0 | 121 | 37.0 | 163 | 49.0 | 20 | 6.1 | 327 | 75 | 0 | 475 |
| 4 | 42 | 1.9 | 301 | 13.7 | 997 | 45.4 | 855 | 38.9 | 2,196 | 127 | 199 | 209 |
| 3 | 53 | 2.4 | 298 | 13.4 | 971 | 43.8 | 892 | 40.3 | 2,214 | 322 | 131 | 97 |
| 2 | 74 | 2.8 | 337 | 12.8 | 1,063 | 40.4 | 1,142 | 43.8 | 2,631 | 243 | 224 | 91 |

We may then consider it fairly well established that none of the largest workers are produced during the first two years of the colony's life, and that the sexually perfect forms are not produced until the colony is at least four or more years old. If it is true that the male forms usually arise from eggs laid by workers, we may add to the above that egg-laying workers do not appear until just preceding the production of winged queens. We then have a rather gradual increase in perfection from the smallest worker produced by the queen the season of her marriage flight to larger workers, then to egg-laying workers and finally to perfect winged females, and if the queen lives throughout this period, and it is altogether likely that she does, the eggs that produce these various forms are all laid by the same queen. An expla-

nation of this is not easy, yet I presume that I shall do no violence if I attempt one.

The most obvious external condition which may be responsible for this phenomenon is the food supply of the colony. During the first years the workers are few and the domestic duties are proportionally large. The permanent home must be established and there is consequently comparatively little time for food gathering, and probably in many cases relations are not readily established with a suitable herd of aphids, so that in all probability the larvæ of these years are scantily fed or are fed a less varied and less concentrated food than that given those that appear when the colony is more mature. During the later years the formicary is well established and there are larger and more powerful workers to make what extensions are necessary. The working force is increased proportionally more than the number of larvæ to be fed. These workers range over a wider field and collect not only more, but a greater variety of food. There can thus be little question that the larvæ of the large colony are better fed than are those of the small one, and since the better feeding is parallel with the production of more perfect forms, it seems only reasonable to believe that there is some relation between them. If it be asked, why do not all the workers of a given season develop into the same size or form, I think that I can say in reply that the food is not equally distributed. I have had numerous instances of a few of the larvæ developing much more rapidly than others in my artificial nests. The winter larvæ when taken were all practically of the same size, and many of them remained unchanged in size for several weeks after being brought into the insectory, while others, usually a small portion of the whole number, soon began to grow quite rapidly.

This leads us to the conclusion that the variations in form are ontogenetic in origin, that the fertilized eggs of the queen are all essentially alike when laid, and each capable of developing into a small worker or a winged queen. This conclusion is supported by a view proposed by Emery in a paper entitled "Die Entstehung und Ausbildung des Arbeiterstandes bei den Ameisen." I quote the following sentences of this paper from Wheeler's "Polymorphism of Ants" (*Bulletin of American Museum of Natural History*, Vol. XXIII., Article I.):

"The peculiarities in which the workers differ from the corresponding sexual forms are, therefore, not innate or blastogenic, but acquired, that is somatogenic. Nor are they transmitted as such, but in the form of a peculiarity of the germ plasm, that enables this substance to take different developmental paths during ontogeny."

Wheeler remarks in connection with this quotation that the view presented has never received the attention that it merits, and I trust that the data that I have brought out in connection with the life-history of a colony may serve to strengthen it appreciably. Wheeler has also elsewhere ("A Neglected Factor in Evolution," *Science*, N. S., Vol. XV., pp. 766-774) referred to the influence of the age and trophic status of the colony on the variability of the polymorphic ants.

DIVISION OF LABOR.

Division of labor among the workers, like their polymorphism, is incomplete; and yet, in the one outdoor colony which I studied, very marked traces of it were seen. This colony, which I shall designate as colony A, lived in a large maple tree which stood on the border of a city block containing but three houses, the rest of the block being vacant, and allowed to grow up in weeds. One hundred and fifty feet away from the nest tree of this colony and just at the rear of one of the houses, stood a cottonwood tree, five or six years old; and near this was a clump of small boxelder trees. The cottonwood was infested with one species of aphid and the boxelders with another. The ants adopted these two "herds" of aphids as their main source of food, but showed a decided preference for those on the cottonwood. At the base of this tree they constructed a temporary chamber, by entering into a crack in the ground and carrying out the particles of earth as they do the particles of wood from their permanent home. After they had used this retreat for a time, I tore it open and, by means of glass plates, constructed a chamber for them somewhat like a Fielde nest, covering it with a piece of orange-colored glass through which I could easily observe what occurred beneath. This the ants readily accepted as equivalent to the one that they had constructed, and used it throughout the summer.

The first aphid appeared on the tree about May 1, 1906, and when I first noticed it a single ant was attending it. Gradually, as the colony of aphids increased in numbers and spread over the tree, the number of ants to be seen there also increased proportionally. My attention was very early called to the fact that, although some of the larger workers (size no. 2, Fig. 3) were often about the base of the tree, they never ascended to the aphids. The work of attending the aphids was performed entirely by workers of size no. 3. After the aphids became abundant I repeatedly saw ants of this size coming from the hole in the ground and ascending the tree to the aphids, and later returning. At the same time numerous workers of size no. 2 were coming from the nest and entering the hole in the ground, and others of this size were leaving this hole for the nest. On the evening of July 20, I made an observation which explained these actions. A no. 3 came down the tree and before entering the ground was accosted by a no. 2 and responded by giving up to her larger sister apparently all that she had gathered above. While their mandibles were interlocked in the process of transferring food the abdomen of the smaller one kept up a constant quivering, jerking motion, seemingly in an effort to regurgitate the last drop of food in her body. After this was over the smaller ones returned to the aphids, and the larger one entered the apartment in the ground as if not yet satisfied to return to the nest. This led me to construct the artificial chamber mentioned above and in this I have seen this process repeated many times. I find, however, that it is seldom that the no. 3 gives all the food that she has to offer to the first no. 2 that approaches her. During the daytime when only very few of the ants were active, a large number of the smaller workers were at rest in the quarters I had constructed for them and not much exchange of food was going on, but when I saw them here just after they had begun their evening's activities, or examined this chamber by means of a light, after dark, as many as two thirds of those in the chamber were paired off in the act of exchanging food. At these times, between the aphid tree and the nest was a caravan of workers going and coming, and these were very largely, though not wholly, of size no. 2. Those returning to the nest had their abdomens distended

until they appeared, at first glance, much larger than those traveling in the opposite direction. Thus, so far as this one colony is concerned, the food was gathered almost entirely by workers of these two intermediate sizes; the one, no. 3, so far as I have observed, without exception, first gathering the fluid from the aphids, and no. 2 principally transporting it to the nest, though aided by some of no. 3.

I have not observed other colonies sufficiently to determine whether this practice is general among them, though it surely cannot be universal for many colonies find their aphids on the same tree in which they live. This was a mature colony of large size and had probably perfected this division of labor gradually as the colony developed in conformity to the conditions that surrounded them.

The work of the two extreme sizes is more difficult to make out, for they are in some way the "house-keepers," that is, they are, during the daytime, at least, about the nest. The smaller ones, size no. 4, are often seen carrying the particles of wood and the empty pupa cases from the nest. Taking into account the immense mandibles of size no. 1, one might suppose that these are the true carpenter ants, and that it is their business to build additions to the formicary; but as has been shown in the tables above, they appear in the colony after it is pretty well established, and then occur in rather small numbers we must at least conclude that they are not the only carpenters in the colony. In general behavior they resemble very much the virgin queens. In the artificial nest they remain constantly in the dark room, and when the colored glass is removed they are among the first to seek shelter and the last to show fight. I have had since capture colony 6, Table III., in a nest which is connected with a feeding-room by means of four glass tubes each about three and a half feet long, three of them coiled and one straight, and I have never seen a no. 1, in the feeding-room, although there are fifty of them in the colony. The queen of this colony died soon after capture, and yet many eggs have been laid, I consequently feel quite certain that the no. 1's are principally egg-layers, and it is probable that along with the development of the ovaries some of the instincts of the queen also appear, and a corresponding lack of certain other instincts possessed by the common workers.

FOOD.

The food of these ants consists principally of the so-called "honey dew," of the aphids, this being supplemented by insect food, and occasionally by plant juices. While they may prefer some species of aphids to others, they are not limited to any one, and seem to be able to make use of all species that infest the aerial parts of plants. I have seen them attending aphids on burdock, on wild lettuce, and on spruce trees, as well as on plants whose sap has a more pleasant taste to us. The aphids are not domesticated as are those of some other species of ants, and I have found no aphids or aphid eggs in any of the nests that I have opened. In October, when the aphids on the cottonwood tree above mentioned were laying eggs, I repeatedly collected leaves to which eggs were attached, and placed them near the base of the nest tree and at various other places in the direct path of the ants, but although I repeatedly saw the ants pass directly over the eggs, they paid no attention to them.

So far as my observations go, their insect food is never taken alive. These ants seem to live peaceably with all creatures so long as the portals of their formicary are not crossed, and they give free admission here to a good many special guests. They do not even attempt to monopolize the herd of aphids which they attend, but seem to admit the equal claim of other species of ants. When a dead insect is found by them, a number of workers gather around it and suck out its fluids, which they then carry to the nest, leaving the dry, chitinous skeleton behind. I have noticed, however, that they nearly always carry the hard chitinous head of an insect into the nest, and I have often wondered why this is done. In the actions of ants living in my artificial nests I think that I have found explanation. After feeding these colonies a number of white grubs, I have noticed that the head is always carried from the feeding-room into the nest. Here it remains for a few days, and then the empty shell, which has been divested of the last particle of soft tissue, is thrown upon the rubbish heap. It may be that in the head is a choice bit of food, possibly the brain of the larva, which is served directly to some special member of the household, or it may be

that some special skill, not possessed by the foraging worker, is required to extract it.

I have frequently seen individuals of *C. pennsylvanicus* feeding on an apple, and on one occasion saw them extract the juice from a large stalk of pie-plant. This material was available to them for some time during the season, but they helped themselves to it only once. I once saw a colony which lived in the trunk of a large ash tree feeding on the pulp of a water-spout of the tree. They had removed almost every particle of material from within the bark for a distance of about a foot, so weakening the sprout that it had bent over. This had been done within a short time, for the leaves above the injury, although wilted, were still green, and a few of the ants were yet working on it when I saw them.

These ants seem to possess great power of husbanding the nutriment within their own bodies. I have kept colony 1, Table IV., in the insectory since January, giving them no food but sugar and water, and yet they have successfully brought to maturity all or nearly all their larvæ, their workers have laid many eggs, and the colony is now, May 10, to all appearances, as healthy as any under my care. The proteid food required for the feeding of the larvæ and for maturing the eggs must have been in store in some form in the bodies of the workers. I have also noticed, with respect to the colonies which I have collected since the few warm days we had in March, that many of them are much larger than any I saw in outdoor nests previous to that time. Very few of these ants have even yet, May 10, been seen out of the nest, and the food upon which the larvæ have grown must have been a surplus of that stored for the purposes of respiration during the winter. I have two colonies, viz., 16 and 12, of Table III., to which I have given no food since April 6. Colony 16 had been given the usual indoor fare since capture up to the time mentioned above, and colony 12 was captured on the day the experiment began. Both colonies are now, May 10, apparently as healthy as any others that I have in confinement.

This faculty adapts them admirably to the conditions of their life, for gathering their food as they do, and being unable to store it otherwise than in their bodies, there is likely to be consider-

able variation in its character, and considerable fluctuation in its amount.

RELATIONS TO LIGHT AND COLOR.

In endeavoring to work out the relations of these ants to light and color I have resorted to experiments modeled after those made by Fielde, Lubbock and others, on other species of ants. I have, however, used slightly different apparatus from that used by either of these investigators. In the first place I constructed a nest of the Fielde type which was twenty-four inches long and nine and one half inches wide, and which contained a hall-way one and one half inches wide, running longitudinally through the center, with six rooms, each 4 by 4 inches, on either side of the hall-way. The outer walls of the nest were bound by black binding paper and the walls between the rooms were made of two pieces of glass with a strip of black paper between them, so that all the walls of each room were perfectly darkened and no light could enter the rooms except through the glass plates placed over them and through the small pieces of glass tubing which formed the entrances from the hall-way. The nest was connected with a feeding-room by means of a piece of glass tubing which led from one end of the hall-way. The hall-way was covered with a strip of clear glass, and as covers for the rooms I used glass plates of the following descriptions :

1. A deep red glass which transmitted only the red rays of the spectrum.
2. A brownish orange glass which transmitted all of the red end of the spectrum including a large part of the green.
3. A green glass which transmitted all of the green rays and a small part of the red.
4. A deep blue glass which transmitted all of the blue end of the spectrum, including a very little of the green.
5. An indigo-blue glass transmitting all colors of the spectrum to some extent, but showing narrow absorption bands in the red and green.

I also used cells containing carbon disulphide to shut out the ultraviolet rays.

With this apparatus I performed the following experiments :

Experiment I.

January 1, 1907. — On one side of the hall glasses were placed on the rooms in the following order : red, orange, green, indigo, blue, clear ; and on the other side in the reverse order, so that the two red glasses were on diagonally opposite corners of the nest. A colony of *C. pennsylvanicus* was introduced into the feeding-room. This colony was just large enough to fill comfortably two of the rooms, and too large to get into one.

January 2. — All ants were settled in the two rooms covered by red glass. The red plates were now exchanged with the two clear plates, and on January 3, all ants were again collected under the red glass. These red plates were now removed from the nest and were replaced by plates of clear glass. On January 4, about one third of the colony were in one room under green glass, another third were under orange, and the remaining third stayed where they were under clear glass for four days, finally joining their companions under the green and orange respectively on January 8. These glasses were now exchanged with the two indigos, and the ants remained unsettled for a whole week of dark, cloudy weather, as many of them remaining under clear glass as under any other. On January 15, I placed double thicknesses of orange glass over two of the rooms, and on January 18 all ants were collected in these two rooms. I now removed the orange glasses from the nest, replacing them with clear glass, and on January 19, after a few hours of bright sunshine, the ants were all collected under the two green glasses. These were then exchanged with clear glass and the ants were again unsettled for a period of six days, when a bright day caused them to settle under the green glasses on January 25. These glasses were now removed from the nest and replaced by clear glass. The nest was then left for twelve days in this condition with only the blue, indigo and clear glass over the rooms, and although there were several bright days during the time, the ants never settled in any one room, but seemed to be endeavoring to escape. On February 6 I replaced two of the clear plates with the two green plates, and on February 8 all ants were collected in these rooms. I then placed the orange plates back on the nest, but no ants collected under them. On February 15 I

placed the red plates back on the nest and the following day about twenty ants were collected under one of them, but not all of the ants removed to the red glass, however, until February 22. The glasses were now arranged as at the beginning of the experiment and the carbon disulphide cells were placed over the two clear plates. The experiment now proceeded as before, with no essential difference in results, until the red, orange and green glasses had been removed from the nest. The green plates were removed on March 8, and two days later all ants were collected under the two disulphide cells. I then returned the green plates to the nest, and the following day ten ants were in the room under one of them. The number that left the disulphide cells for the green gradually grew until, on March 17, all had done so.

Experiment II.

This colony was now removed from the nest and, after the latter was thoroughly cleaned, another colony of *C. pennsylvanicus* containing a large number of winged queens and males was introduced. The glass plates were again arranged as at the beginning of the experiment and the disulphide cells were placed over the clear plates. The colony would have filled about three of the rooms, but they scattered out and occupied eight of them, omitting entirely, however, the two indigos and the two blues. The nest was left as first arranged from March 20 to May 12, and some ants were seen at all times in each of the eight rooms in which they first settled, except a few days while the disulphide cells were removed. During all this time only occasional stragglers were ever seen under the blue or the indigo plates.

Experiment III.

A number of the queens of the colony used in experiment II. were removed for other experiments and the colony was reduced in size until it could easily occupy two of the rooms, and then, on May 12, the nest was taken into a room which admitted no light from the outside and which was supplied with an arc light of four hundred and eighty candle power. The nest was placed about three feet below the arc light, and a little to one side so as to avoid the shadows of the lamp. The glass plates were

arranged as in experiment I., and the disulphide cells were placed over the clear plates. The ants immediately collected under the red plates after the arc light was turned on. These plates were then exchanged with the two blue plates, and twenty-five minutes later the ants were again under the red plates. These plates were then replaced by clear plates, and thirty minutes later all ants were collected under the two orange and one of the green plates. The orange plates were again exchanged with the blue, and in twenty-five minutes the ants were under the two green and one of the orange plates. The green plates were then removed from the nest and thirty-five minutes later all ants were under the two orange plates. These were then removed from the nest and forty minutes later all ants were under the two disulphide cells. The two disulphide cells were now placed over the blue plates and in twenty-five minutes all ants were collected under them. Next the cells were moved to the indigo plates and in thirty-five minutes all ants were again under them. The cells were then placed back on the clear plates and in thirty-five minutes the ants were again under them. The red plates were then placed back on the nest, and two hours later some of the ants were still under the disulphide cells, although most of them had moved to the red plates.

These results indicate plainly that, when forced to choose between light of different wave-lengths, these ants have a decided preference for the red or longer rays and a decided dislike for the ultraviolet rays. The last part of experiment III. also indicates that they prefer the red rays to the blue and violet rays. In these respects these ants seem to agree perfectly with the ones which Lubbock experimented upon ("Ants, Bees and Wasps," pp. 211 to 217) and also with those of Miss Fielde ("Notes on An Ant," Philadelphia Academy of Science, Vol. 54, pp. 614 to 625).

Experiment IV.

Twenty-five workers of *C. ferrugineus* were cooled until they were inactive and then their eyes were carefully painted with a mixture of liquid glue and lamp black. They were then placed in a Fielde nest consisting of two rooms, four by four inches, which were joined by a narrow passage-way. One room was

covered with a red glass plate, such as described in experiment I., and the other with clear glass. The nest was now exposed to the arc light. At the beginning, the ants were all placed under the red glass, and after the light was turned on, the glass plates were changed about. The ants showed some uneasiness, and yet remained under the clear glass for two hours, seeming to be utterly ignorant of the fact that they were exposed to bright light. As a check on this experiment a similar number of workers from the same colony were placed in a similar nest, but their eyes were not painted. By changing the glass plates I was able to cause them to move from one room to the other fifteen times in thirty-five minutes. This makes it evident that the effects observed are due to the light as perceived through the eyes.

Experiment V.

Twenty workers and five queens of *C. pennsylvanicus* were placed in a hollow cylinder formed by rolling up a strip of fine wire screen and stopping the ends with corks. A centigrade thermometer was thrust through a hole in one of the corks so that the bulb was in the center of the cylinder. The cylinder was now held for an hour about four inches from the arc light. In this position the thermometer registered about 40° C. The ants were exceedingly active all the time, and showed no ill effects afterwards. I have found by other experiments that these ants are able to endure a temperature of 40° C. indefinitely without serious effects, but that they are very suddenly killed when the temperature reaches 46° C.

These results indicate that these ants are adapted to withstand very intense light which is rich in ultraviolet rays, and so, evidently, their nocturnal habits are not a result of necessity, but of simple preference.

There are always some of the workers busy during the daytime of the active season, but the vast majority remain quietly in the nest, and then, a few minutes after sunset, the whole colony seems to awake and the night's labors begin.

August 12, 1906, I observed the outdoor colony *A*. I began counting the ants which left the temporary nest at the base of the aphid tree to collect food from the aphids, just as the sun

disappeared from sight. During the first eighteen minutes I counted only twenty-two ants, and then, as if by a sudden signal, the procession began to move, and during the following eighteen minutes I counted five hundred and twenty-two ants, and about this time the supply in the nest below seemed to be almost exhausted. A little before I stopped counting, large numbers of the larger workers began to arrive from the nest tree and to enter the temporary nest at the base of the tree. I have observed this colony repeatedly at different times during the night, and as late as two o'clock in the morning, and have always found them very active.

ARCHITECTURE AND ECONOMIC RELATIONS.

McCook describes in detail the architecture of a colony of carpenter ants which he found inhabiting a corner beam of an old mill. ("A Guild of Carpenter Ants," *Harper's Monthly*, July, 1906.) In the same article he discusses serious injuries to forestry and lumber interest which have been reported to have been done by the carpenter ants, and he also reports railroad accidents which were thought to have been caused by carpenter ants weakening the timbers of bridges.

Dr. E. P. Felt, state entomologist of New York, also accuses the large, black carpenter ants of doing much injury to forests. ("Insects Affecting Forest Trees," Seventh Report, New York State Commission of Forest, Fish and Game, p. 522.) In this

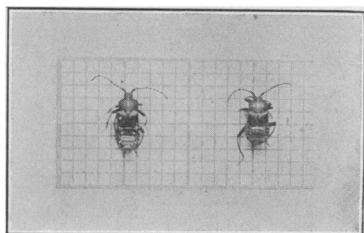


FIG. 4. Two specimens of *Xenodusa cava*.

article he shows in cuts the very different styles of architecture followed by the ants in elm and in balsam and supposes that the difference is due to the different structures of the two woods.

The observations which I have made while collecting the colonies represented in the tables of this paper lead me to believe

that the carpenter ants are guiltless of much that they are charged with and also that they may scarcely be credited with having a distinctive architecture of their own. In solid wood they follow the burrows of wood-boring larvæ almost exclusively making very slight changes as long as the wood is solid. In Fig. 4 is shown a piece of wood taken from a large ash tree which was hollow for a few feet at the base, and which was inhabited by a large colony of *C. ferrugineus* and numerous wood-

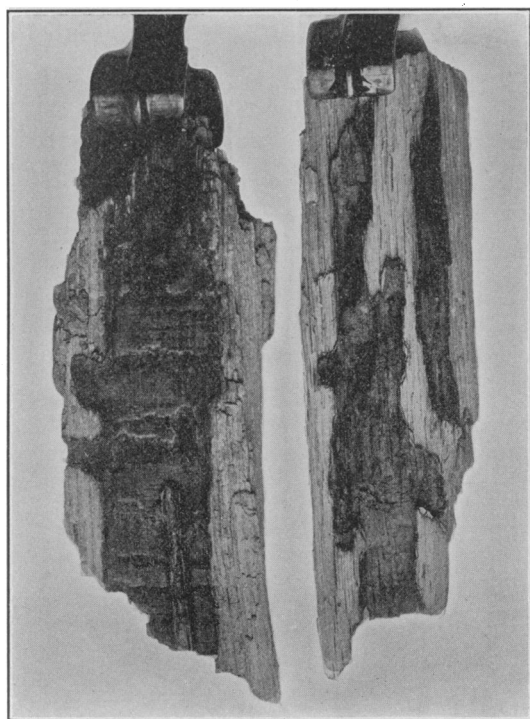


FIG. 5. View of a gallery of *C. ferrugineus* as seen in a radial section of decayed oak.

FIG. 6. Same as Fig. 1, as seen in tangential section.

boring larvæ. Both the ants and the wood-bores had entered from the inside and were working outward toward the living parts of the trunk. The ants were living entirely in the unaltered galleries of the larvæ. All that they had done was to clean out

the voided wood that the larvæ had left in the burrows. As the wood gradually decays and in cases where the ants follow larvæ that bore in decayed wood they do enlarge the galleries and shape them into chambers which are more or less characteristic, but even here the style of the architecture is determined largely by structure of the wood and the instinct of the particular larva followed. The influence of the structure of the wood is shown in Figs. 5 and 6. Fig. 5 shows a radial section of decayed oak in which the more durable medullary rays formed a limit to the gallery in one direction and in Fig. 6 is shown a tangential section of the same wood in which the dense summer wood of an annual ring forms the limit in the other direction. Many observations similar to these have convinced me that these ants do not build their own galleries in solid wood. They either follow the wood-bores or work in badly decayed wood and if this conclusion is true their economic importance must be extremely slight.

GUESTS AND PARASITES.

Probably the most distinguished and interesting guests which have been found with ant colonies are certain Lomechusini, several species of which are very common guests with the ants of continental Europe. This family is represented in North America by the single genus *Xenodusa*, and the best known representative of the genus is *X. cava*, Fig. 7. Wheeler, in a review of the observations made on this beetle ("Polymorphism of Ants," *Bulletin American Museum of Natural History*, Vol. XXIII., pp. 35-40), shows that, so far as reported, only five persons, viz.: Leconte, Blanchard, Muckermann, Schwarz and himself, have ever seen it and each of these only rarely. Schwarz found it with *C. pennsylvanicus*, and Blanchard with a colony of large black ants which were probably of the same species. No one has before seen it with *C. ferrugineus*. By referring to Tables III. and IV. of this paper, it will be seen that I have found it to be quite abundant in this region, and by a comparison of these two tables, it will be seen that the beetle seems to prefer *C. ferrugineus* as a winter host. Wassmann and Wheeler are of the opinion that the beetle simply hibernates with these larger ants and then in the spring migrates to the nests of some smaller ants

as a summer host. In fact Wheeler found, July 1, 1905, six larvæ of *X. cava* in a nest of *Formica incerta*, and since the European relatives of the beetle are found mainly with this genus



FIG. 7. Galleries in solid ash wood which were inhabited by *C. ferrugineus*.

of ants, it seems quite probable that the summer host of *X. cava* may be some one or more of the *Formicas*. During the month of June, 1907, it was my hope to discover the summer host and I accordingly opened a good many nests of *Formica* in the vicinity of the woods in which I found the beetle most abundant, but was unable to find a trace of either adult beetle or of larvæ. I did, however, find adult beetles in the nests of *C. ferrugineus* at differ-

ent times during the month. On June 10, I opened two nests seeing five beetles in one and three in the other; on June 20, I found four beetles in a nest of these ants and on June 30, I opened a nest and saw two of the beetles. These may have been a few stragglers which had not migrated because of some disability yet I could not see any signs of imperfection in them. Since Wheeler found larvæ on July 1, it seems quite probable that at least some of the beetles spend the summer also with the winter host.

The beetles are always royally received into the nests of the two varieties of ants that I have been studying. I have kept them all winter in artificial nests with the ants, have transferred them from one colony to another and have placed them in the nest with colonies which had none in their out-door nests, and they were always received and cared for. I have repeatedly seen the ants licking them and feeding them, and when the beetles strayed out to the feeding-room of the nest the ants would pick them up and carry them back to the nest.

Another guest or parasite which I have found abundantly with the colonies of *C. pennsylvanicus* is a small red mite, which, according to Nathan Banks, to whom I sent some mounted specimens, is an undescribed species of *Uropoda*. I have not been able to determine whether these are parasitic or merely attached to the ants for the purpose of transportation, but am inclined to think the former, as was also Mr. Banks. They were always attached to the ants at the joints of the legs, or on the underside of the joint between the head and thorax and were probably extracting their nourishment through the thin nonchitinous membranes of these regions. It seems a little peculiar that the ants permitted them to stay there, for evidently they could easily have removed them. It is possible, however, that the mites secured this attachment after the ants became inactive from the cold, for I collected them all during the winter and noticed that the mites disappeared within two or three days after being brought into the insectory.

Besides these I have found numerous other insects which live either in the nest or in very close proximity to it and seem to live peaceably with the ants. Among these are various staphy-

linid beetles, several species of Blattidæ, and the adults of the wood-boring larvæ. Other ants are also often very close neighbors of the species I have studied. I have found two colonies of small ants in chambers which were connected on all sides with those occupied by the larger ants. One of these was a colony of *Myrmecina americana*, which I found with a colony of *C. ferrugineus*, and the other a colony of *Monomorium pharaonis*, which I found with a colony of *C. pennsylvanicus*. The insectory is badly infested with this latter species and they have helped themselves liberally to the food that I have given my ants, and have especially thrived on the dead ants which my colonies threw upon their rubbish heaps. These little ants are not noticed by the larger ones, and doubtless in the natural nests they subsist largely by picking up the "crumbs" about the formicaries of the larger species.

INSTINCTS AND INTELLIGENCE.

The many remarkable feats performed by ants in the round of their daily life have led observers to form various conclusions as to the parts played by instincts and intelligence respectively, in controlling their movements. Lubbock, on the one hand, concludes that ants rank next to man in the degree of intelligence possessed ("Ants, Bees and Wasps," p. 1), and on the other hand, Wassmann endeavors to show that they are absolutely void of pure intelligence ("Psychology of Ants").

On this subject I have made the following observations and experiments:

Observation 1.—On the evening of August 1, 1906, I planned to count the number of workers of outdoor colony *A*, which passed a certain point between the nest and the aphid tree, in a given time. In order to do so I cleared away the weeds so that I might see them more easily. I soon noticed, however, that ants were collecting on both sides of the place where I had disturbed the path, and they refused to cross the disturbed area. Considerable excitement seemed to prevail on both sides, and the number kept increasing, especially on the side toward the nest. Some of these returned to the nest and some of the others returned to the aphid tree. Finally, after about thirty minutes, when approximately one hundred ants were assembled on the

side toward the nest, this group began to advance slowly into the disturbed territory. After much retracing of steps they succeeded in about three minutes in crossing this area, which was only about one foot in diameter, and they then hurried on their way unhesitatingly.

Observation 2.—About fifty feet of the path of this colony from the nest to the aphid tree lay through a dense weed patch. Early in the summer I had smoothed out with a hoe a narrow path in a fairly direct line from the nest to the aphid tree, and by repeatedly passing along this path myself, I kept it worn smooth all summer. I repeatedly observed that the ant caravan used this path only at points where it happened to coincide with a perfectly direct line between the point at which they entered the weed patch and the point at which they emerged from it.

On the afternoon of August 4, 1906, some men came with a plow and tried to plow the weeds under. The weeds were three or four feet high, and when the plowing was finished the lot seemed to me an impassable barrier to the movement of the ants. That evening, as the ants began to pour forth from the nest for their night's work, great excitement ensued when they reached the edge of the plowed ground, which was about five feet from the nest. Soon a space about one foot wide and reaching from the nest to the plowed ground was literally black with ants, all running back and forth and behaving very much as people do in case of a fire in a city. After about twenty minutes of confusion the vanguard began to advance slowly into the plowed ground, and in just two hours they had reached the other side. During all this time about one hundred and fifty ants which had started from the aphid tree to the nest were collected near the border of the plowed ground, but not one of them ventured as much as an inch into it. The next day and evening they were traveling back and forth just as if nothing had happened, and the path that they followed was so straight that when I stretched a line across between the two points of entrance no ant was seen to be more than five inches to either side of the line anywhere along the course. A decided curve was made in the path, however, after reaching smooth ground on the side toward the aphid tree.

Experiment I.

December 24, 1906, I connected a Fielde nest containing a colony of *C. pennsylvanicus* with a feeding-room by means of a series of five glass tubes, each about six inches long. Five days later, when the ants had become accustomed to these tubes, I turned one of the sections of the tube end for end and ants passed through in both directions without seeming to notice the change. Next I removed one of the sections and replaced it with a new piece of tubing of the same size. At this time three workers were in the feeding-room, and soon one of them started to go to the nest. She went hurrying along the tube until she came to the new section, when she suddenly stopped and began feeling cautiously about. She then made several trips to the feeding-room and back to the new section, but did not venture a full length into it. While she was continuing in this way another worker came from the nest and she too came to a sudden stop on reaching the new section of the tube. She examined it carefully and then, without returning to the nest, proceeded cautiously through it. Here she met her friend who had formerly discovered the change, and after they had exchanged antennal greetings, the two returned to the nest. This experiment was repeated a number of times and always with the same results, that is, those ants which were in the feeding-room always refused to cross the new section until they had met some friends directly from the nest, while those coming directly from the nest always crossed the new section, at least, after making one trip back to the nest.

Experiment II.

The same nest as above was connected with the feeding-room by means of a glass tube four feet long which had been bent at the center to form an angle of about 110° . The ends were bent in the opposite direction, so that by slipping the ends of this tube over the smaller tubes which led from the nest and feeding-room respectively, and by rotating the larger tube about the smaller ones as axes, I could vary the elevation over which the ants must travel in passing from nest to feeding-room. The tube was allowed to lie flat on the table usually, and at intervals I would raise it up so as to cause a steep incline. When this was done

ants which were in the feeding-room would not hesitate to pass through it, but they would invariably try to walk on the side which was lowermost when in the usual position.

Experiment III.

I have repeatedly taken a stick and made a narrow mark in the earth across the path of the ants from the nest to the aphid tree and have observed that only very few of the ants going from the nest to the aphid tree seem to notice it, while nearly all those going in the opposite direction would stop and examine the mark carefully for some time, and some would return to the aphid tree rather than cross the mark.

These experiments show clearly that the ants behave differently when traveling from the nest than when returning to it. They are seemingly willing to venture into new territory when traveling away from the nest, because of something akin to a consciousness that they can at any time retrace their steps and find the nest, while when traveling toward the nest the link is broken when the surface of the earth is disturbed across their path. This may be either because the continuity of the outgoing trail is destroyed, or because the appearance of things with which they are familiar is altered.

Observation 2 seems to indicate quite strongly that these ants possess a sense of direction and an unusual power of using it under unfavorable circumstances. The rough ground all matted with weeds must have appeared to them much as a mountain region over which a cyclone had torn the forest to shreds would appear to us, and yet they made a straight path across it in the darkness. Their determination to cross this hazardous region at once seems also to imply that had some realization of the interests at stake and some memory of the direction in which the goal lay.

Experiment IV.

A Fielde nest containing a large colony of *C. pennsylvanicus* was connected with a feeding-room by means of a system of four glass tubes, each one half inch in diameter. One of these tubes was straight, another was bent into a vertical loop, another into a horizontal loop, and the fourth was arched so as to form a steep

incline. All four were brought together at the ends into triangular-shaped vestibules. A single tube led from one of these to the nest, and one from the other to the feeding-room. After this apparatus had been set up for forty-eight hours and the ants had become somewhat accustomed to the system of tubes, I placed in the feeding-room about two hundred larvæ which had been taken from the nest two hours before. Two small workers were in the tubes when the larvæ were placed in the feeding-room. They were apparently lost, for they divided their time between remaining perfectly motionless as if trying to gain their bearings, cleaning their antennæ, and running frantically about in the tubes. After about twenty minutes of such conduct, one of them entered the feeding-room and discovered the larvæ. She examined them carefully with her antennæ and then, with more excitement than before, renewed her search for the nest. She ran wildly about the system of tubes and the feeding-room for twenty-two minutes, and then found her way from the vestibule to the nest. On reaching the nest she ran against five of her companions very much as ants do when they first discover a stranger in the nest, and she then returned directly to the larvæ, passing through the straight tube. The five friends which had been greeted in this peculiar way turned around a time or two and then followed their informant immediately into the tubes, all passing into the straight tube, and three of them going directly to the larvæ in the feeding-room. The other two seemed to lose the trail in the second vestibule, and began running about the tubes. Each of the four who reached the larvæ began carrying them into the straight tube, and after making three trips from the larvæ to this tube, the original discoverer of the larvæ returned to the nest and, by the same behavior as before, succeeded in bringing three others to the scene of activity. Before all the larvæ were removed from the feeding-room five ants had returned to the nest for help and each time secured it. Thirty ants were in this way called into service, yet not an ant left the nest which had not been greeted in this peculiar way. After all the larvæ had been carried into the straight tube, the ants began carrying them into the nest, and as the larvæ arrived in the nest other ants joined in the work, so that the tubes were soon alive with ants.

This experiment was repeated a number of times and each trial gave unmistakable evidence that the ant which discovered the larvæ in some way conveyed the intelligence to others. I have also had similar evidence of communication when I placed the carcass of a white grub in the feeding-room of a colony that had been deprived of animal food for some time. In the succeeding trials of this experiment, however, it never happened again that all the larvæ were returned to the nest through the straight tube. They were as often carried over the vertical loop as through any other tube, and this happened just as frequently after the ants had used the tubes for three or four months as at first. The ants always work as if in great haste to get the larvæ back to the nest, and it seems that if they had had any discretion whatever, they would have chosen the shorter and less difficult route. In one instance, however, I watched an ant while making six trips from a cluster of larvæ which had been carried into the straight tube. Three of the six times, when returning to the larvæ, she entered the arched tube from the vestibule and proceeded until she came to the incline and then each time turned about and found the straight tube and the larvæ. She seemed to remember that the larvæ were in the straight tube and so knew that she was in the wrong tube when she came to the incline. She also seemed not to be tracking herself as she returned to the larvæ.

Experiment V.

Three islands were formed by inverting two-inch Petri dishes in four-inch ones and filling the larger ones with water. One of these islands, which I will designate as *A*, was connected with the feed-room of the apparatus used in experiment IV., by means of a glass tube which was bent in such a way as to be partly immersed in water in a Petri dish. This made it impossible for the ants to crawl back to the feeding-room over the tube and escape to the table. The other islands, which I will designate as *B* and *C* respectively, were connected with island *A* by means of bridges of cardboard eight inches long and one half inch wide. *B* was placed in a direct line with the tube leading to *A*, and *C* was placed at right angles to the tube, opposite *A*.

Larvæ taken from the colony in the nest were placed on *B* and

the bridge to *C* was removed. After about one hour a small worker discovered the tube and cautiously followed it to *A*, and then passed over the bridge to *B*, where she discovered the larvæ. After examining them carefully she started to find her way back to the nest. After passing through the feeding-room and into the vestibule she entered the tube with the horizontal loop and went as far as the loop and then turned about to the vestibule and thence went through the arched tube and to the nest. In the nest she saluted four of her friends in the manner described in experiment IV., and returned to the larvæ followed closely by the four friends saluted and no others. In going to the larvæ she passed through the arched tube by which she had returned to the nest, but instead of following the diagonal path by which she had previously crossed the feeding-room, she followed around the sides of this room until she came to the entrance to the tube leading to island *A*. Each of the five ants on arriving at *B* picked up a cluster of larvæ, carried them to the place where the tube leading from *A* passed under the toweling of the feeding-room, dropped them there as in a place of temporary safety, and returned for more. While the ants were in the tube with the third load, I moved the bridge from *B* to *C* and placed a new bridge leading to *B*. The first and second ant to come back to *A* passed over the new bridge to *B*, but the other three, after turning around once or twice on *A*, passed down the old bridge to *C*, retracing their steps, however, a few times before finally reaching it. They then returned to *A* and finally found the larvæ again. I now allowed them to pass over this bridge to *B* about eight times and then again moved this bridge to *C*, taking away the one there already, and placing a new bridge from *A* to *B*. This time all five of the ants passed directly over the new bridge to *B*, and I could not see that any of them detected the change. After all the larvæ had been removed from the island to the tube, three of the five ants began carrying them to the nest while the other two returned to the nest empty-handed for help, and my observations ended in the confusion that soon followed.

This experiment was repeated a number of times; and while there were a few variations in results, those recorded in detail

above are typical. The principal variations are the following: Sometimes instead of waiting for an ant to find the larvæ, I took one directly from the nest and put her with them. When this was done the ant invariably picked up a cluster of larvæ and sought to find a temporary place of safety for them. In this she sometimes succeeded, and at other times she brought the larvæ back to the others on the island and then found the way home before again touching them. In no instance, however, did an ant which had found the larvæ herself attempt to carry them away until she had made a trip to the nest.

In one trial the ant which found the larvæ called on eight of her friends to help before she started to lead them to the larvæ. While she was doing this two of the first she had saluted started for the larvæ ahead of her and went directly to them, following exactly the route over which their informant had returned to the nest.

If I changed the bridge from *B* to *C* and replaced it with a new one while the first discoverer of the larvæ was on her first trip to the nest, those that followed her back invariably went to *C* and, not finding the larvæ there, they often returned to the nest and seemed to give up the search as if they had been falsely advised. But, although the original discoverer sometimes also followed her old trail to *C*, I never knew one which had really seen the larvæ to give up searching until she found them again.

I think that these experiments and observations fully warrant the following conclusions:

1. These ants have some means of inter-communication. A. Bethe has endeavored to show that all so-called communication among ants may be explained by odors carried by the informants and perceived by those saluted (*Dürfen wir den Ameisen und Bienen Psychische Qualitäten zurechnen*). But in this case I do not see how the ants saluted could have known that the odor of the larvæ which the informant may have borne was not received from the larvæ in the nest. It is perhaps possible that the larvæ removed from the nest give off some special odor which is a signal of distress and which may be conveyed to the nest by the informant, but I think this far less probable than the other explanation.

2. These ants are capable of tracking themselves and others of the colony, but they are not capable of distinguishing the direction in which the trail was first laid down.

3. They do not depend entirely on following trails in finding their way, but are guided often by a kind of memory of the location of things, and probably depend as a last resort on a sense of direction.

4. They ordinarily pay very little attention to trails when traveling from the nest.

5. They give no evidence, in these operations, of anything akin to reason.

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